African Invertebrates Vol. 44 (1) Pages 175–184 Pietermaritzburg August, 2003

The maxillary organ gland: Description of a new head gland in *Scutigera coleoptrata* (Chilopoda, Notostigmophora)

by

Gero Hilken[1], Claudia Brockmann[2] and **Jörg Rosenberg[3]**

([1]Central Animal Laboratory, University Clinicum Essen, Hufelandstraße 55, D-45122 Essen, Germany, gero.hilken@uni-essen.de; [2]Zoological Institute and Zoological Museum, University of Hamburg, D-20146 Hamburg, Germany; [3]Department of Animal Physiology, P. O. Box 102148, Ruhr-Universität Bochum, D-44780 Bochum, Germany)

ABSTRACT

The present study describes a new head gland in *Scutigera coleoptrata* using light and electron microscopy. This multicellular complex gland is located at the dorsal side of the maxillary organ and is therefore called the 'maxillary organ gland'. This gland is composed of numerous secretory units, each of which is made up of four different cell types: Two secretory cells are attached to a single intermediary cell that mediates between the secretory cells and two different canal cells (a proximal and a distal canal cell). The distal canal cell passes through the cuticle. The cuticular wall of the whole gland enclose a large secretion reservoir. A common cuticular duct drains the secretion into the maxillary organ. Similar complex epidermal glands are hitherto not described in Chilopoda.

The function of the maxillary organ gland in relation to the maxillary organ is discussed. The secretions of the maxillary organ gland support the function of the maxillary organ as a cleaning organ. The secretion of this gland is assumed to spread over the trichoma of the maxillary organ by capillary forces. Legs and antennae that pass along the trichoma will be moistened by the secretory material of the gland. Additionally, the secretion of the gland may contain antibacterial or antifungal substances to protect the numerous annulations of the antennal flagellum and the tarsal articles.

INTRODUCTION

The Notostigmophora have a distinct position within the Chilopoda. Besides the specialized tracheal lungs (Hilken 1994 1997 1998) they have a unique maxillary organ (Haase 1884). Both structures are autapomorphic features that prove the monophyly of the Notostigmophora. However, besides these two complex elements, notostigmophoran centipedes possess a remarkable number of glandular structures in the head region. There has been considerable confusion about the glandular structures in the anterior body regions of centipedes. Plateau (1878) was the first who systematically examined exocrine glands (*glandes antérieure*) within the head capsule of Chilopoda (except the Notostigmophora). However, the first detailed description of head glands was given by Herbst (1891) for Scutigeromorpha, Lithobiomorpha, and Scolopendromorpha. He proposed the name 'head glands' and classified the glands according to their duct openings as system I-V. Duboscq (1898) pointed out that the descriptions of the glands of the head and the anterior trunk differ from one author to another. The most detailed accounts of these glands are those of Fahlander (1938). Using anatomical and histological characteristics, this author differentiated head glands, vesicular glands of the anterior segments, and complex multicellular glands.

The highest number of exocrine glands within the head and the anterior segments occur in the Notostigmophora (Fahlander 1938; Manton 1965):

(a) Head glands: two pairs of buccal glands; one pair of mandibular glands (Fahlander 1938 [= ‘hypopharynx gland’, *sensu* Manton 1965]); paired maxilla I glands; paired maxilla II glands;
(b) Two pairs of vesicular glands with large cavities open antero-laterally under the edges of the tergites of the poison claw and the leg 1 segment, respectively;
(c) Complex glands which are grouped around a pair of apodemes at the base of the second maxillae.

The study of the ultrastructural organization of the maxillary organ of *Scutigera coleoptrata* (Linné, 1758) revealed an additional complex multicellular gland at the dorsal side of the maxillary organ. This complex gland is described here for the first time and is termed the ‘maxillary organ gland’.

MATERIAL AND METHODS

Two specimens of *S. coleoptrata* were collected by the first author in July 1996 around Banyuls-sur-Mer, France at 42°29' N, 3°7' E. The specimens were kept in glass boxes (15 cm x 8 cm x 15 cm) filled with 1 cm garden soil and 2 pieces of moistened (tap water) blotting paper (15 cm x 15 cm each). The animals were fed with wingless *Drosophila melanogaster* and *Musca domestica*. Specimens were killed with CO_2, cut into several parts and preserved as described below.

Light and transmission electron microscopy (TEM)

Segments of *S. coleoptrata* were fixed in Bouin for two days (Gregory 1980, modified), washed in 70 % ethanol and embedded in LR-WHITE (LR-WHITE-soft grade, London Resin Co. Ltd.). Semithin sections (0.5–1 um; Autocut, REICHERT) were stained with toluidin blue (Trump *et al*. 1961; modified: toluidin blue share 1 %). Sections were studied using a DMSL-Leica microscope.

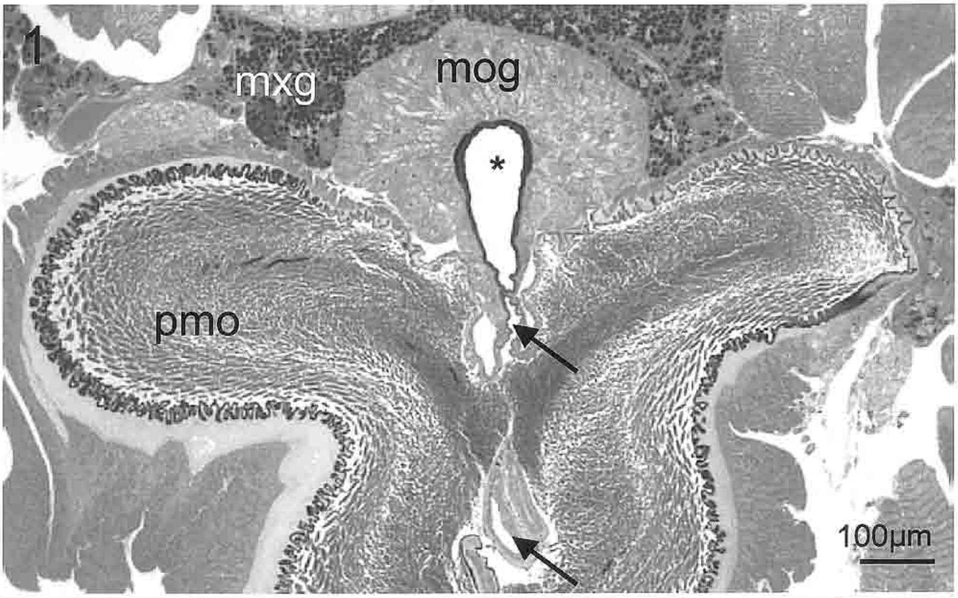
For TEM investigation heads of *S. coleoptrata* were fixed in 2.5 % glutaraldehyde/ cacodylate buffer pH 7.2 or phosphate buffered (0.1 M) paraformaldehyde (4 %), containing 15 % saturated picric acid and 0.08 % glutaraldehyde. They were postfixed with 1 % OsO_4 in the same buffer and after alcohol dehydration embedded in Epon, Ultrathin sections were stained with uranyl acetate and lead citrate and studied using a ZEISS EM 902 A electron microscope.

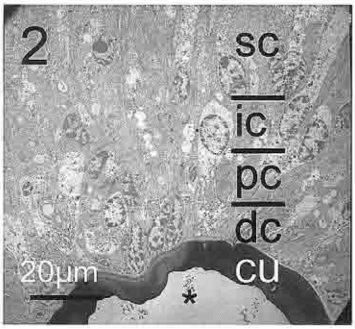
RESULTS

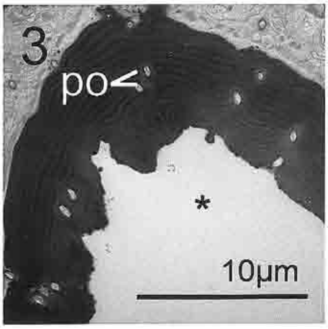
General organisation and histology

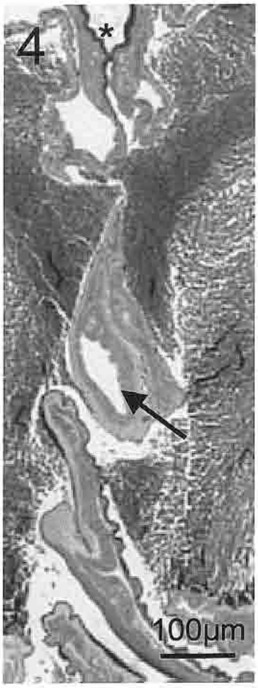
There are two areas of deeply invaginated cuticle on the dorsal surface of the coxosternite of the first maxilla, covered with different kinds of trichomes. Haase (1884)

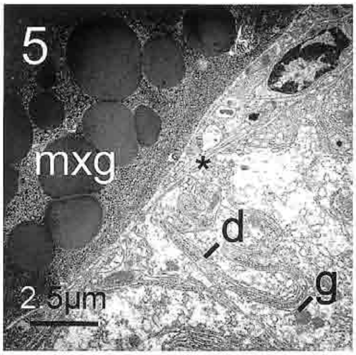
Figs 1–6. Maxillary organ gland of *Scutigera coleoptrata*. 1. Light microscope (LM) general view of maxillary organ, showing maxillary organ gland with numerous trichomes. *pmo* pouches of the maxillary organ, *mog* maxillary organ gland, *mxg* part of the maxillary 1 gland, * secretion reservoir, arrows point to the conduction canal. 2. Cross section of the epithelium of maxillary organ gland, showing the different regions of cell types of the glandular units. *sc* region of secretory cells, *ic* region of intermediary cells, *pc* region of proximal canal cells, *dc* region of distal canal cells, a distinct cuticle (*cu*) borders the wide secretion reservoir (*) surrounded by the glandular epithelium. 3. Cuticle of maxillary organ gland with numerous pores (*po*) of glandular units, * secretion reservoir. 4. Secretion reservoir (*) and conducting canal of maxillary organ gland (arrow, LM). 5. Proximal part of a secretory cell with dictyosomes (*d*) and ER. * basal lamina, *mxg* maxillary 1 gland, *g* granulum. 6. Distal part of secretory cells with their extracellular cavities (*). *za* zonula adhaerens, *ic* extracellular cavity of intermediary cell filled with microvilli.

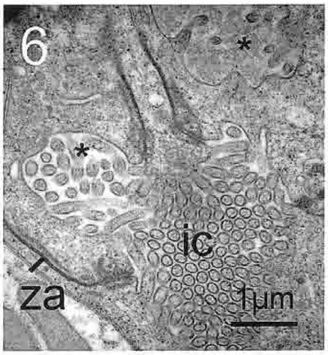

1
mxg
mog
*
pmo
100µm


2
sc
ic
pc
dc
cu
20µm
*


3
po
*
10µm


4
*
100µm


5
mxg
*
d
g
2.5µm


6
*
*
ic
za
1µm

termed this organ 'maxillary organ'. This sac-like organ (Fig. 1) originates from the inner lobe of maxilla I. The two invaginated pouches of left and right maxilla I are connected dorsally by the huge glandular epithelium of the maxillary organ gland (Fig. 1). The gland extends for over two-thirds of the length of the maxillary organ. The maxillary organ gland, round in shape, is lined by a thick (10 µm) cuticle (Figs 1–3). The lateral walls of the glandular epithelium surround a huge secretion reservoir (Figs 1, 3). The reservoir opens ventrally by a cuticular duct which crosses the maxillary organ medially (Figs 1, 4). In light microscopy its epithelium appears undifferentiated (LM, Figs 1, 4). This duct opens between the suture of the two coxosternites of the first maxillae.

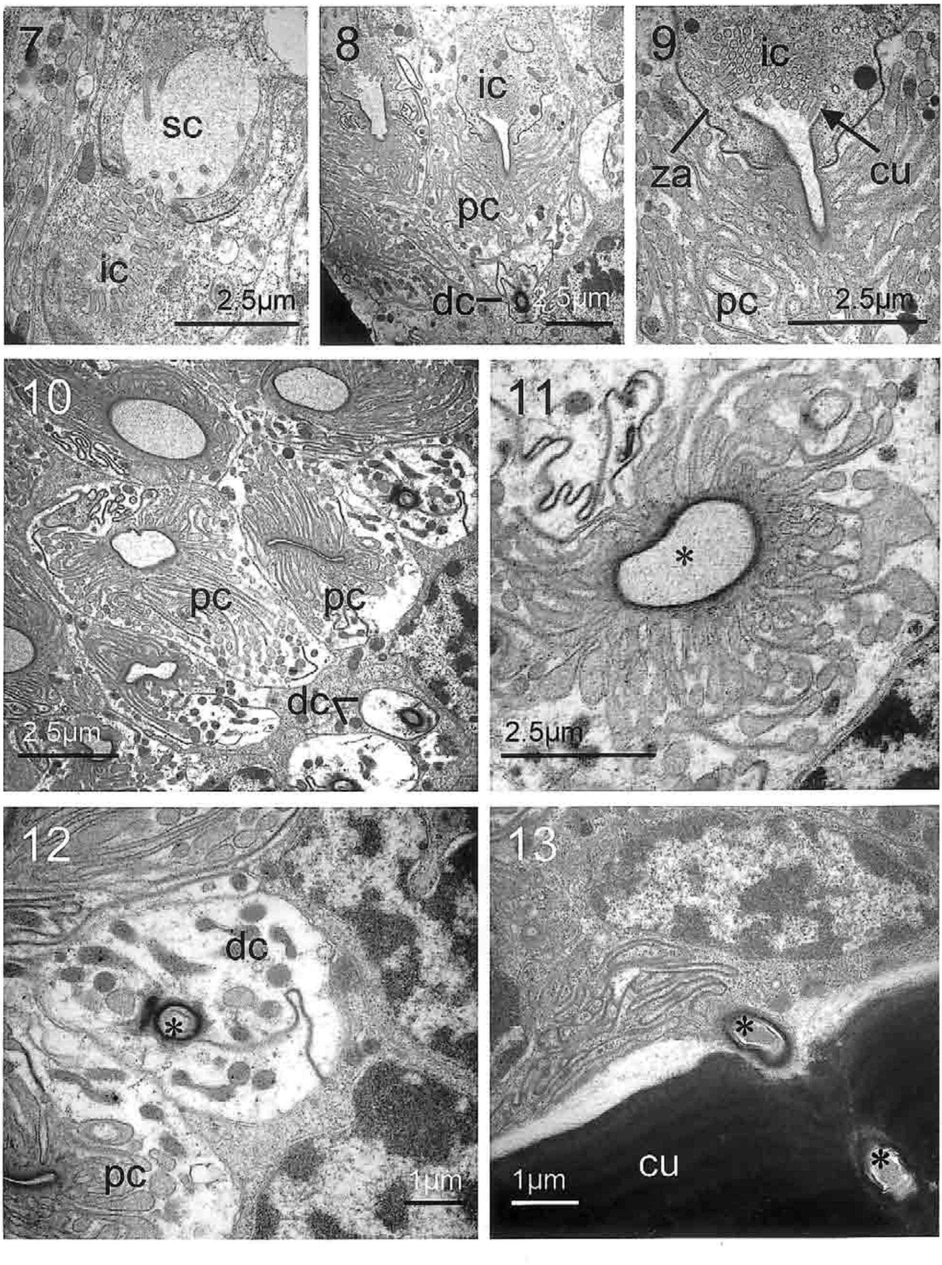
Ultrastructure

The epithelium of the glandular complex (up to 60 µm high) is covered by a distinct cuticle up to 8.5 µm in width, with a wide lamellated endocuticle and a narrow epicuticle (Figs 1–3). The epithelium is separated from the hemolymph by a continuous basal lamina (Fig. 5). The gland complex is composed of numerous secretory units, each of which consists of two secretory cells attached to an intermediary cell, which is followed by a proximal, and a distal canal cell, the latter passing through the cuticle (Fig. 14). No nerves were detected between the secretory units.

Secretory cell. The voluminous egg-shaped secretory cells are situated in the proximal region of the complex gland and taper distally. In their peripheral parts, these cells are filled by rough endoplasmic reticulum (RER), often arranged in parallel stacks, intermingled by vesicular ER. Numerous dictyosomes are present (Fig. 5). The voluminous nuclei are generally situated in the median part of the cells. Numerous small mitochondria occur. In the proximal part of the cell, secretory vacuoles are present (Figs 5, 7). Mostly they appear electron lucent. Each secretory cell is invaginated distally. The apical plasma membrane forms several, short microvilli, which surround a widened extracellular cavity (Figs 6, 7). The content of the secretory vacuoles is discharged into these cavities.

Intermediary cell. Intermediary cells are distributed in the upper third of the complex maxillary organ gland (Fig. 2). This cell connects the extracellular cavity of each secretory cell and the extracellular part of the following proximal canal cell (Fig. 8). The intermediary cell surrounds the apices of two secretory cells (Fig. 6). Both cells are connected via zonulae adhaerentes (Fig. 6). The apex of the narrow intermediary cell has a distinct microvillus border bounding a widened extracellular cavity (Figs 6–9). Only the most distal part of the cavity is lined by a cuticular intima that continues to the cuticle of the following proximal canal cell (Figs 8, 9). The cytoplasm contains free ribosomes and parts of vesicular ER; mitochondria are rare; and the nucleus is small.

Proximal canal cell. The intermediary cell is connected to the proximal canal cell by large zonulae adhaerentes (Fig. 9). The canal cell itself forms a cuticular duct up to 1.5 µm in diameter which continues from the distal part of the intermediary cell (Fig. 9). The narrow cuticle appears homogenous, electron lucent and is surrounded by an osmiophilic layer (Fig. 11). The cuticular duct is surrounded by many deep infoldings of the apical cell membrane forming a so called 'end-apparatus' (Fig. 10; compare Noirot & Quennedy 1974) which disappears distally (Fig. 10). The extracellular space between the infoldings is filled with homogeneous material of low density (Fig. 11).



Figs 7–13. Maxillary organ gland of *Scutigera coleoptrata*. 7. Transition between secretory cell (*sc*) and intermediary cell (*ic*). 8. General view of intermediary cells (*ic*) and connecting proximal (*pc*) and distal canal cells (*dc*). 9. Transition between intermediary cell *(ic)* and proximal canal cell (*pc*) with its apical infoldings. Note the cuticular lining (*cu*) of the conduction canal in the most distal part of the intermediary cell. 10. Distal part of maxillary organ gland with several cross sections of the proximal (*pc*) and distal (*dc*) canal cells and their cuticular ducts (*). 11. Cross sectioned proximal canal cell with apical infoldings and cuticular duct. The asterisk points. 12. Cross section of the distal canal cell (*dc*) with its cuticular duct (*). (*pc*) proximal canal cell. 13. Part of distal canal cell with its conducting canal (*) passing through the cuticle (*cu*) of the maxillary organ.

The light cytoplasm contains, beside longish mitochondria, only small profiles of rough ER; the nucleus is round (Fig. 2).

Distal canal cell. A little below the cuticle, the proximal canal cell is replaced by the distal canal cell (Figs 10, 12). Its cuticular ductule (0.5 µm in diameter) runs through the cuticle and opens into a huge secretion reservoir (Figs 3, 13). The electron dense cytoplasm is filled with numerous free ribosomes and a few mitochondria. The nucleus is shaped irregularly (Figs 10, 12).

DISCUSSION

Head glands have only rarely been described in Myriapoda. Despite careful examinations of the glands of the head and the anterior region by Herbst (1891) and Fahlander (1938) and some studies on the maxillary organ (Haase 1884; Heathcote 1885), the maxillary organ gland of *S. coleoptrata* described here has not previously been noted. The number of head glands and glands of the anterior region of *S. coleoptrata* is now nine. Most of these glands are multicellular exocrine glands which consist of a secretory unit and an unbranched tubular duct. The paired salivary glands are connected with the anterior intestine: *Lateral buccal glands* open into the oral cavity, *median buccal glands* open into the anterior region of the pharynx, and *mandibular glands* are situated within the hypopharynx and open laterally on the hypopharnyx into the oral cavity (Fahlander 1938; Manton 1965). The other glands do not open into the alimentary canal: The paired *first maxillary gland* opens immediately anterior to the basal part of the first maxilla; its secretory part lies ventral to the nerve cord and stretches up to the second leg-bearing segment. The *paired second maxillary gland* lies between the forcipular segment and the first leg-bearing segment. These glands open on both sides of the head behind and under the coxae of the second maxillae. In the anterior segments there are two pairs of so-called vesicular glands with large cavities. The *first vesicular gland* with its small secretory part opens postero-dorsally to the opening of the second maxillary gland and the maxillary nephridium. The *second vesicular gland* is one of the largest glands in the anterior part of the body and opens anterior-laterally under the edge of the tergite of the first leg (Fahlander 1938; Manton 1965). In addition to the above-mentioned exocrine glands, Fahlander (1938) described a huge complex of gland packets ('Komplex von *Drüsenpaketen*') at the base of maxilla II, as a unique cellular gland grouped around a pair of apodemes and covered by a cuticle.

The here described maxillary organ gland is a complex multicellular gland, covered by a cuticle. The whole gland is composed of numerous exocrine glandular units which consist of four different cell types. The glands are derived from the epidermis, as the whole maxillary organ gland is covered by a cuticle and the canal cells retain their relationship to it. Therefore the maxillary organ gland can be characterised as a complex exocrine epidermal gland. Each glandular unit corresponds to the 'type-3 glands' according to the classification of epidermal gland cells in insects by Noirot & Quennedy (1974) and Quennedy (1998). Type-3 glands are composed of several cells connected to the cuticle by a cuticular duct draining the secretion outside.

There is great variability in the organisation of the epidermal glands of Chilopoda. They are composed of two different cell types only, where secretion material of a

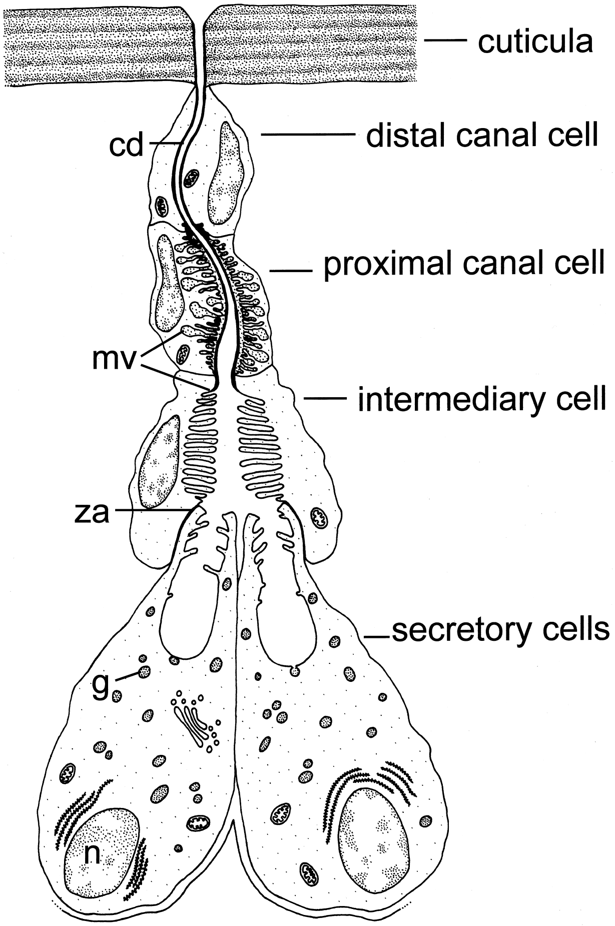


Figure 14. Schematic representation of one glandular unit of maxillary organ gland of *Scutigera coleoptrata*. Two secretory cells are attached to the intermediary cell. The proximal and distal canal cells secrete a cuticular efferent duct (*cd*), passing the cuticle of the maxillary organ gland.*g* grana, *n* nucleus, *mv* microvilli, *za* zonula adhaerentis.

single secretory cell is discharged by a single canal cell. This is the case in some epidermal glands of some Lithobiomorpha, which form telopodal glands. In other cases they are associated with sensilla trichodea or with the organ of Tömösvary, or are situated in the vicinity of the coxal organs (Tichy 1973; Keil 1975; Rosenberg 1994). In Geophilomorpha they form the ventral glands (Hopkin & Anger 1992; Turcato & Minelli 1990). It is obvious that in *S. coleoptrata* the canal cell of the maxillary organ gland has distinct infoldings of the distal cell membrane and is therefore considered to be secretory. In a more complex glandular unit, the epidermal glands are formed by three cell types: the secretion of a single secretory cell is discharged by two conducting cells. This is the case in the exocrine glands surrounding the coxal organs of Chilopoda in which the innermost canal cell exhibits microvillar infoldings around the conducting canal (Rosenberg 1985; Rosenberg

& Greven 1996). In *S. coleoptrata* three cell types form the exocrine eye gland between the ommatidia (Müller *et al*. 2003).

The present study demonstrates the very complex structure of the maxillary organ gland, whose glandular units represent a further type of epidermal gland. Here, four different cell types constitute the functional glandular unit. Two secretory cells are connected via an intermediary cell to two canal cells. A secretory function of the innermost canal cell is indicated by infoldings of the distal cell membrane around the conducting canal. The extracellular cavities found in both secretory and intermediary cells appear to be too small to function as a reservoir of released secretion material. The extraordinarily large reservoir surrounded by the maxillary organ gland takes on this function in *S. coleoptrata*.

Similar complex epidermal glands are not known in Chilopoda, but have been found in Diplopoda, where they form pyloric glands and pyloric valve glands (Schlüter 1979 1980), anal glands (Schlüter 1982) or postgonopodial glands (Juberthie-Jupeau 1976; Juberthie-Jupeau & Tabacaru 1968). However, the glandular units differ from those of the maxillary organ gland: the intermediary cells exhibit no microvillar border and the innermost canal cell lacks apical infoldings around the conducting canal. In the tentorium gland of *Polyxenus lagurus* only a single conducting cell is present, and the intermediary cell exhibits a microvillar border (Nguyen Duy-Jacquemin 1978). A cuticle, which lines the extracellular cavity of secretory cells of insect epidermal gland cells (Noirot & Quennedy 1974, Quennedy 1998) has never been observed in Chilopoda and Progoneata.

The function of the maxillary organ remains unclear. Haase (1884) and Heathcote (1885) regarded it as an auditory organ. This assumption was rejected by Manton (1965), who thought the very elaborate distendable maxillary organ has a cleaning function, through which the long trunk legs and antennae are repeatedly passed. The ultrastructural examination proves that sensory cells are absent along the epithelium of the maxillary organ, suggesting it is not a sensory organ. The presence of numerous trichomes on the surface of the maxillary organ suggests that the trunk legs and antennae may be cleaned mechanically, as proposed by Manton (1965). The secretions of the maxillary organ gland may improve the function as a cleaning organ. The secretion of this gland is assumed to spread over the trichoma by capillary forces. Legs and antennae that pass along the trichomes will be moistened by the secretory material of the gland. Additionally, the secretion of the gland may contain antibacterial and antifungal substances to protect the numerous annulations of the antennal flagellum and the tarsal articles. It has been observed that antennae and legs are regularly drawn through the maxillary organ. It is also possible that the trichomes of the maxillary organ serve as a large surface area to distribute the gland secretions that may alternatively have a pheromonal function. Further studies are needed to clarify these questions.

ACKNOWLEDGEMENTS

The authors are very grateful to Prof. Dr H.-W. Denker for providing access to the electron microscopy facility of the Institute of Anatomy, University of Essen. Dorothee Schüncke, Institute of Anatomy, University of Essen, is especially acknowledged for helpful technical support. We would like to thank Prof. Dr G. Heusch and Ina Konietzka (Institute of Pathophysiology, University of Essen) for providing access to their light microscope, and Dr John Lewis (Taunton, Somerset, United Kingdom) and an anonymous referee for their valuable comments on the manuscript.

REFERENCES

DUBOSCQ, O. 1898. Recherches sur les chilopodes. *Archives de Zoologie Expérimentale et Générale 3. Serie*. **6**: 481–655.

FAHLANDER, K. 1938. Beiträge zur Anatomie und systematischen Einteilung der Chilopoden. *Zoologiska Bidrag* **17**: 1–148.

GREGORY, G. E. 1980. Insect nervous system. *In*: Strausfeld, N. J. & Miller, T. A., eds, *Neuroanatomical techniques*. New York: Springer pp. 75–95.

HAASE, E. 1884. Schlundgerüst und Maxillarorgan von *Scutigera*. *Zoologische Beiträge* **1**: 97–108.

HEATHCOTE, F. G. 1885. On a peculiar sense organ in *Scutigera coleoptrata,* one of the Myriapoda. *Quarterly Journal of Microscopical Science* **25**: 253–260.

HERBST, C. 1891. Beiträge zur Kenntnis der Chilopoden (Drüsen; Coxalorgan; Gefäßsystem und Eingeweidenervensystem). *Bibliotheca Zoologica* **3** (9): 1–43.

HILKEN, G. 1994. Struktur und phylogenetischer Ursprung der Tracheensysteme von *Scutigera coleoptrata* (Chilopoda, Notostigmophora). *Verhandlungen der Deutschen Zoologischen Gesellschaft* (Jena) **87**(1): 90.

——— 1997. Tracheal systems in Chilopoda: A comparison under phylogenetic aspects. *Entomologica Scandinavica* Supplement **51**: 49–60.

——— 1998. Vergleich von Tracheensystemen unter phylogenetischem Aspekt. *Verhandlungen des Naturwissenschaftlichen Vereins Hamburg* **37**: 1–91.

HOPKIN, S. P. & ANGER, H. S. 1992. On the structure and function of the glue-secreting glands of *Henia vesuviana* (Newport, 1845) (Chilopoda, Geophilomorpha). *In*: Meyer, E., Thaler, K., & Schedl, W., eds, *Advances in Myriapodology, Proceedings of the 8th International Congress of Myriapodology*. *Berichte des Naurwissenschaftlich-Medizinischen Vereins in Innsbruck,* Supplementum **10**: 71–80.

KEIL, T. 1975. Die Antennensinnes- und Hautdrüsenorgane von *Lithobius forficatus* L. Eine licht- und elektronenmikroskopische Untersuchung. Dissertation FB 23, FU-Berlin 1–61.

JUBERTHIE-JUPEAU, L. 1976. Fine structure of postgonopodial glands of a myriapod *Glomeris marginata*. *Tissue & Cell* **8**: 293–304.

JUBERTHIE-JUPEAU, L. & TABACARU, I. 1968. Glandes postgonopodiales des Oniscomorphes (Diplopodes, Myriapodes). *Revue ´d Écologie et de Biologie du Sol* **4**: 605–618.

MANTON, S. M. 1965. The evolution of arthropod locomotory mechanisms. Part 8. Functional requirements and body design in Chilopoda, together with a comparative account of their skeleto-muscular systems and an appendix on a comparison between burrowing forces of annelids and chilopods and its bearing upon the evolution of the arthropodan haemocoel. *Journal of the Linnean Society London (Zoology)* **46**: 251–483.

MÜLLER, C. H. G., ROSENBERG, J. & MEYER-ROCHOW, V. B. 2003. Hitherto unknown exocrine gland within the complex eye of *Scutigera coleoptrata* Linneus, 1758 (Chilopoda, Notostigmophora). *African Invertebrates* **44** (1): 185–197.

NGUYEN DUY-JACQUEMIN, M. 1978. Ultrastructure des glandes du tentorium (Glandes "cérébrales") de *Polyxenus lagurus* (Myriapode: Diplopode, Pénicillate). *Annales Des Sciences Naturelles 12. Sér* **20**: 339–356.

NOIROT, C. & QUENNEDY, A. 1974. Fine structure of insect epidermal glands. *Annual Review of Entomology* **19**: 61–80.

PLATEAU, F. 1878. Recherches sur les phénomènes de la digestion et sur la structure de l'appareil digestif chez les Myriapodes de Belgique. *Memoires de l Academie Royale de Belgique* **42**: 1–94.

QUENNEDY, A. (1998): Insect epidermal gland cells: Ultrastructure and morphogenesis. *In*: Harrison, F. W. & Rice, M. E., eds, *Microscopic anatomy of invertebrates*, Vol. 11A Insects pp. 177–207.

ROSENBERG, J. 1985. Untersuchungen zur feinstrukturellen Organisation und Funktion der Coxal- und Analorgane bei Chilopoden. *Bidragen tot de Dierkunde* **55**: 337–344.

——— 1994. Fine structure of epidermal glands in vicinity to the coxal organs of *Lithobius forficatus* (Chilopoda). *Acta Biologica Benrodis* **6**: 37–47.

ROSENBERG, J. & GREVEN, H. 1996. Coxal organs of Chilopoda: the exocrine glands in *Lithobius forficatus*. *In*: Geoffroy, J.-J., Mauries, J.-P. & Nguyen Duy-Jacquemin, M., eds., *Acta Myriapodologica*. *Mémoires du Muséum National d´histoire Naturelle (Paris)* **169**: 403–409.

SCHLÜTER, U. 1979. The ultrastructure of an exocrine gland complex in the hind-gut of *Scaphiostreptus* sp. (Diplopoda: Spirosteptidae). *In*: Camatini, M., ed., *Myriapod biology*. Academic Press pp. 143–155.

——— 1980. Die Feinstruktur der Pylorusdüsen von *Polydesmus angustus* Latzel und *Glomeris marginata* Villers (Diplopoda). *Zoomorphology* **94**: 307–319.

——— 1982. The anal glands of *Rhapidostreptus virgator* (Diplopoda: Spirosteptidae). I. Appearance during the intermoult cycle. *Zoomorphology* **100**: 65–73.

Tichy, H. 1973. Untersuchungen über die Feinstruktur des Tömösvaryschen Sinnesorgans von *Lithobius forficatus* L. (Chilopoda) und zur Frage seiner Funktion. *Zoologisches Jahrbuch Anatomie* **91**: 93–139.

Trump, B. F., Schmuckler, E. A.& Benditt, E. P. 1961. A method for staining epoxy sections for light microscopy. *Journal of Ultrastructure Research*. **5**: 343–348.

Turcato, A. & Minelli, A. 1990. Fine structure of the ventral glands of *Pleurogeophilus mediterraneus* (Meinert) (Chilopoda, Geophilomorpha). *In*: Minelli, A., ed., *Proceedings of the 7th International Congress of Myriapodology*. Leiden: Brill pp. 165–173.